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REVIEW PAPER

Knowledge shortfalls on the edge effects on amphibians and reptiles: research gaps and trends

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Abstract
Landscape transformation reduces the size of remaining natural patches and intensifies edge effects. These effects alter environmental conditions and vegetation structure, degrading remnant habitats. Amphibians and reptiles (herpetofauna) are especially vulnerable to edge effects because of their ecophysiological traits (e.g., critical temperatures, dehydration rates), making them valuable indicators of habitat change. We evaluated biodiversity knowledge shortfalls across 100 studies published from 1968 to 2025 that assessed edge effects on herpetofauna worldwide. Our results reveal pronounced geographic gaps: research is concentrated in the Nearctic (33%) and Neotropical (32%) regions, whereas the Palearctic, Sino-Japanese, Oriental, and Madagascan regions, as well as highland systems more broadly, remain underrepresented. Within regions, studies are concentrated at low elevations (74% conducted below 500 m a.s.l.) and in tropical moist broadleaf forests and temperate broadleaf–mixed forests (47% and 35%, respectively). Analysis of taxonomic bias shows a predominance of squamates and anurans (48 and 47 studies, respectively), whereas Testudines are rarely studied, and Gymnophiona and Crocodylia are entirely absent. Regarding the response variables analyzed in the studies, the literature most consistently addressed Prestonian-related dimensions, with 93% of studies focusing on abundance or occupancy-related variables. In contrast, major gaps remain in the study of functional traits and diversity (Raunkiæran shortfall; 11 studies), thermal tolerances (Hutchinsonian shortfall; 9 studies), biotic interactions (Eltonian shortfall; 8 studies), and evolutionary history (Darwinian shortfall; only 1 study on phylogenetic diversity). Studies are strongly biased toward edge interfaces between exotic pastures and old-growth forest interiors, or between secondary forests and old-growth forest interiors, while rapidly expanding urban, infrastructure-related, and agroforestry edges remain largely understudied. By integrating geographic, taxonomic, and ecological response variables, this synthesis reveals multidimensional knowledge shortfalls that constrain our ability to predict species responses to anthropogenic edges and to develop effective conservation strategies for vulnerable herpetofauna in fragmented landscapes.

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Introduction

The transformation of natural ecosystems by human activities stands as one of the main drivers of biodiversity loss, particularly through deforestation and habitat conversion (Wilson et al. 2016; Curtis et al. 2018). This process has caused the rapid decline of forests (~4.06 billion ha, covering 31% of the Earth's land area) and savannas (~2 billion ha, covering 15%), two of the most extensive terrestrial biomes, particularly in tropical and subtropical regions (Laurance et al. 2014; FAO 2024). The accelerated deforestation of native forests, together with the afforestation and land-use conversion of naturally open ecosystems such as savannas and high-elevation non-forest systems, has become a global conservation concern due to the critical role biodiversity plays in sustaining the ecosystem services on which humans depend (Naeem et al. 2016; Reis et al. 2024). Although substantial data on biodiversity responses to anthropogenic landscape transformation are already available (Pfeifer et al. 2017; Hudson et al. 2017), these data must be better integrated to identify general patterns and to guide long-term monitoring of key variables in a rapidly changing world (Gonzalez et al. 2023).

Driven primarily by deforestation and afforestation, habitat fragmentation is a significant outcome of terrestrial landscape transformation. This process divides formerly continuous natural habitats into smaller and more isolated patches embedded within an anthropogenic matrix (Fahrig 2017). This pattern is most directly driven by the expansion of intensive land uses (e.g., croplands, pastures, plantations) and linear infrastructure (e.g., roads), which remove or dissect native vegetation and often restrict movement and dispersal across the landscape (Murcia 1995; Haddad et al. 2015). In contrast, the abandonment of some agroecosystems may promote secondary succession and increase the complexity of vegetation structure locally, potentially altering edge extent and habitat configuration—and, in some cases, partially improving connectivity for native species—depending on landscape context (Dent and Wright 2009). A critical byproduct of habitat fragmentation is the creation of sharp boundaries between natural habitat remnants —that is, native ecosystems with relatively intact structure and composition (e.g., old-growth or mature secondary forests, native savannas or grasslands, wetlands, riparian corridors, and montane forests)— and human-modified areas, referred to as edge effects (Laurance et al. 2002; Harper et al. 2005). These edge effects significantly impact biodiversity, as nearly 20% of the world's remaining natural habitats are located within 100 m of an edge, 50% within 500 m, and 70% within 1 km (Haddad et al. 2015). Moreover, habitat fragmentation and its associated edge effects are expected to intensify over the next decades (Laurance et al. 2014; Betts et al. 2019), further exacerbating the ongoing decline in biodiversity (e.g., Luedtke et al. 2023).

Edge effects shape both biotic and abiotic conditions, serving as critical drivers of ecological change in fragmented landscapes (Murcia 1995; Laurance et al. 2007). However, the scope and intensity of these effects vary widely, influenced by several factors such as edge age, the contrast between remaining native vegetation and surrounding land cover, the origin of the edge (whether natural or anthropogenic), the type of adjacent anthropogenic matrix, and the natural vegetation cover type used for comparison (Ewers and Didham

2006; Pfeifer et al. 2017). For example, matrix permeability and microclimatic conditions can either mitigate or exacerbate edge-related stressors, leading to species responses that are highly context-dependent (Gascon et al. 1999; Ries et al. 2004). Given this complexity, synthesizing general patterns in species groups sensitive to biotic and abiotic factors related to edge effects is crucial (Schneider-Maunoury et al. 2016; Pfeifer et al. 2017) to highlight significant knowledge gaps (Hortal et al. 2015) and help steer future research on edge effects in transformed landscapes.

Herpetofauna—amphibians and reptiles—perform essential ecological functions, such as pest regulation and energy transfer between trophic levels (Valencia-Aguilar et al. 2013), yet they are particularly sensitive to habitat transformation (Nori et al. 2015; López-Bedoya et al. 2022; Iglesias-Carrasco et al. 2023) due to their physiological constraints. As ectothermic vertebrates, their physiological reliance on temperature and humidity makes them exceptionally vulnerable to microclimatic changes along habitat edges (Watling and Braga 2015; Nowakowski et al. 2018). These sensitivities, coupled with their relatively limited dispersal abilities and strong site fidelity, render herpetofauna as prime bioindicators of edge-related habitat modifications (Huey 1991). Evidence syntheses support this general expectation, although conclusions vary depending on the spatial and taxonomic scope of the review. For instance, Schneider-Maunoury et al. (2016) focused on Neotropical amphibians and reptiles, finding that median edge effects extend 250 m into the forest interior. In contrast, Pfeifer et al. (2017) conducted a global assessment across multiple vertebrate classes, reporting that forest-core species reached peak abundances only beyond 200–400 m from high-contrast edges. The magnitude and direction of these effects are shaped by biome, elevation, edge origin and contrast, and the type of adjacent matrix (e.g., pastures vs. roads vs. urban infrastructure). Consequently, “reducing edges” as a broad conservation goal fails to specify which edges or taxa should be prioritized in policy and land-use planning (Urbina-Cardona et al. 2024).

Despite the growing body of research, including quantitative reviews on Neotropical herpetofauna (Schneider-Maunoury et al. 2016), global assessments of habitat-edge impact on tetrapods (Pfeifer et al. 2017), and global analyses of edge effects on species richness (Willmer et al. 2022), a comprehensive systematic synthesis focused on herpetofauna is still lacking. Existing syntheses emphasize abundance and matrix–edge–interior contrasts, while other ecological response variables relevant to management—such as demographic performance, functional vulnerability, thermal sensitivity, and biotic interactions—remain poorly summarized. To address this, we present the first global-scale systematic review of edge effects on herpetofauna and expand the synthesis beyond abundance to include under-explored ecological dimensions (e.g., interactions, functional diversity, population metrics, and ecophysiological responses). We then apply the biodiversity “knowledge shortfalls” framework (Hortal et al. 2015) as a diagnostic tool to map where evidence is currently robust and where critical gaps persist. By identifying these knowledge deficits, we provide a foundation to prioritize future research efforts across more diverse biomes, elevations and matrix contrasts. Filling these empirical gaps is prerequisite for developing evidence-based decisions grounded in appropriate regional contexts (e.g., which edge contrast require buffering, which matrices should be managed as highest-risk interfaces, and where targeted monitoring/research is needed before generalizing management recommendations across regions or taxa).

Specifically, to quantify gaps in edge effect studies, we aimed to: (Objective I) evaluate the geographic patterns by analysing the distribution of the study sites across zoogeographic regions, biomes, countries, and elevational ranges; (Objective II) quantify the taxonomic biases by assessing the representation of herpetofauna taxa at the class and order levels; (Objective III) identify patterns and research gaps in the ecological response variables used to assess edge effects, addressing the Prestonian, Eltonian, Hutchinsonian, Raunkiæran, and Darwinian shortfalls; (Objective IV) integrate geographic, taxonomic, and ecological response variables to identify multidimensional knowledge shortfalls, using these interactions as a proxy for the Wallacean shortfall and to highlight additional biases and gaps in edge-effect research; and (Objective V) assess the representation and diversity of edge contexts by quantifying the origin of edges (natural vs. anthropogenic), the types of adjacent anthropogenic matrices, and the interior control/reference habitats used.

Methods

Literature search

The process of literature selection and retrieval was based on the PRISMA methodology (Page et al. 2021). We conducted our literature search using EBSCOhost, JSTOR, ProQuest, ScienceDirect, Scopus, Web of Science and Google Scholar, focusing exclusively on peer-reviewed articles published between 1910 and 31 December 2025. In each database, we used the following search queries (in English and Spanish) targeting the title, abstract, and keyword sections: (anole OR squamat OR reptile OR herpet* OR frog* OR toad* OR salamander* OR snake* OR lizard* OR lacertilia OR turtle* OR crocodilian* OR crocodile* OR caecilian* OR testudin* OR skink* OR anfibio* OR rana* OR sapo* OR salamand* OR tadpole OR cecilia OR caudata OR anura* OR apoda OR amphib* OR gymnophiona OR lagart* OR serpiente* OR ofidi* OR tortuga* OR ophid* OR amphisb* OR sauria OR serpentes) AND ("edge effect*" OR "distance to edge" OR ecotone* OR "forest edge*" OR "distance from the edge" OR "edge of forest" OR "forest patch edge" OR "habitat edge").

Document exclusion criteria

A total of 3,512 records were retrieved from the databases and were reduced to 1,113 after removing 2,399 duplicates (Supplementary Material Figure S1). We first screened titles and abstracts to remove records that did not focus on amphibians or reptiles or did not address habitat edges. We then assessed the full texts of 615 articles for eligibility. At this stage, studies were retained only if they: (i) examined edge effects (*sensu* Murcia 1995), defined as ecological changes across the transition zone where two adjacent habitat types meet—either between native ecosystem remnants and anthropogenic land covers or between two natural ecosystems—creating abiotic and biotic gradients that can modify species distributions, interactions, and population processes at habitat boundaries; and (ii) employed a comparative sampling design specifically to test edge-related responses in amphibians or reptiles. Eligible designs included comparisons between native interior vs. edge or, in cases where interior conditions were absent or not sampled (e.g., in highly transformed landscapes), comparisons between the native edge vs. the adjacent matrix (e.g., anthropogenic land covers or secondary vegetation). We excluded, during full-text assessment, studies that investigated fragmentation metrics (e.g., patch size or isolation) without an explicit edge contrast, as well as descriptive natural-history reports of “edge use” (e.g., annotated checklists, herpetological notes, short communications) lacking comparative sampling between habitat positions, because such studies do not allow inference about the magnitude or direction of edge effects. The final database comprised 100 peer-reviewed articles on edge effects in herpetofauna, published between 1968 and 2025 (see Supplementary Material Figure S1 for the PRISMA flow diagram). Hereafter, we refer to each article as a study.

Data overview

For each selected study, we assessed biodiversity knowledge gaps following the framework proposed by Hortal et al. (2015). Specifically, we examined the Wallacean shortfall (incomplete knowledge of geographic distributions), the Prestonian shortfall (scarcity of data on species abundance and population dynamics), the Raunkiæran shortfall (lack of information on functional traits and life-history characteristics), the Hutchinsonian shortfall (gaps in tolerance to environmental conditions), the Eltonian shortfall (limited knowledge of biotic interactions), and the Darwinian shortfall (insufficient understanding of species evolution and phylogenetic relationships). In addition, we quantified taxonomic bias in the literature by assessing the representation of herpetofauna taxa across class and order levels. Applying this multidimensional framework allows for a precise diagnosis of where research efforts on edge-effects are concentrating and where critical blind spots remain.

To address geographical biases, we extracted from each study the following information: (i) country; (ii) zoogeographic region (e.g., Afrotropical, Neotropical, Oriental; *sensu* Holt et al. 2013); (iii) biome type (e.g., tropical moist broadleaf forest, tropical savanna; *sensu* Olson et al. 2001, and Dinerstein et al. 2017); and (iv) elevation (grouped into 500 m bands from 0 to 3000 m above sea level (a.s.l.); no studies occurred between 1500 and 2000 m a.s.l.).

To quantify taxonomic bias in the literature, we classified each study according to its focal taxon at two hierarchical levels: Class (Amphibia or Reptilia) and Order (Anura, Caudata, Gymnophiona, Squamata, Testudines, and Rhynchocephalia). We then quantified the number of studies per taxonomic group. The ecological response variables measured in each study were classified into 16 non-exclusive categories: occupancy, reproduction, dispersion, bioacoustics, species richness, abundance, community composition, parasitism, thermal ecology, population structure, dietary ecology, individual survival, body condition, functional traits, functional diversity, and phylogenetic diversity. Reproduction was retained as a separate category because, in the studies reviewed, reproductive status was typically used as a design factor (e.g., gravid vs. non-gravid females), whereas the main response variables were demographic or performance-related outcomes (e.g., dispersal or egg/tadpole survival) rather than reproductive traits measured as functional traits. Other categories initially searched for in the studies (such as morphology and anatomy, infectious diseases, ethology; Camacho-Rozo and Urbina-Cardona 2024) were not present in any of the studies and were therefore not included in the subsequent analyses.

We linked ecological response variables to knowledge shortfalls (Hortal et al. 2015) as follows: Prestonian—occupancy, abundance, population structure, and individual survival; Eltonian—parasitism and dietary ecology; Hutchinsonian—thermal ecology; Raunkiæran—

body condition, functional traits, and functional diversity; and Darwinian—phylogenetic diversity. Because phylogenetic diversity explicitly quantifies the amount and relatedness of evolutionary history represented in biotic communities, it can detect whether edge-driven community turnover involves non-random loss or reshuffling of lineages (consistent with phylogenetic niche conservatism), thereby assessing how edge effects affect evolutionary heritage, even if contemporary evolutionary change is not directly measured (de la Sancha et al. 2023).

For each study, we extracted information on the types of vegetation cover analyzed as a study site context, including: (i) edge origin (natural or anthropogenic); (ii) interior control habitat type: old-growth forest, restored areas, secondary forest, degraded forest (primary forest with selective logging), xeric shrublands, sand dune; and (iii) the types of adjacent matrices: annual crops, cacao plantations, coffee plantations, sugarcane plantations, (exotic and native) forestry plantations, exotic pasture, cities, native open habitat (e.g. meadow, savannah), oil palm plantations, roads and water bodies. We standardized habitat cover classification based on study area descriptions and existing categorization frameworks proposed by Dent and Wright (2009), Dinerstein et al. (2017), Curtis et al. (2018), and López-Bedoya et al. (2022).

A single study could encompass multiple categories, often evaluating both amphibians and reptiles (e.g., Urbina-Cardona et al. 2006; Gallmetzer and Schulze 2015), different anthropogenic matrices bordering the edge of remaining native cover or edge cover types (e.g., De Maynadier and Hunter 1998; Santos-Barrera and Urbina-Cardona 2011; Ferreira et al. 2016), or various ecological response variables (e.g., Sifers et al. 2001; Semlitsch et al. 2007; Gallmetzer and Schulze 2015; Ferreira et al. 2016).

Quantitative and qualitative analysis

We employed heat maps to illustrate the association between pairs of categorical variables (e.g., zoogeographic region, biome, elevation, ecological response variables, and taxonomic levels when used in interaction analyses) using a continuous colour gradient scale. For each analysis, categories were first ordered by frequency, publication counts were square-root transformed, and resemblance among categories was calculated using a Bray-Curtis similarity matrix. We then computed Whittaker's index of association to quantify the strength of association represented in the heat maps (Clarke and Gorley 2015). This workflow was applied to: (Objective I) assess geographic patterns across zoogeographic regions, biomes, countries, and elevation bands; (Objective II) quantify taxonomic biases; (Objectives III and IV) evaluate how taxa and ecological response variables were distributed across geographic gradients to identify multidimensional gaps; and (Objective V) compare edge contexts by relating adjacent matrix types (natural vs. anthropogenic and specific land-cover classes) to reference/control native vegetation types. All heat-map analyses were conducted using PRIMER v.7.0.13 software (Clarke and Gorley 2015).

Additionally, we used a Voronoi treemap to visualize hierarchical patterns in study frequency, with polygon size proportional to the number of publications (Camacho-Rozo and Urbina-Cardona 2024). The treemap was generated in Carrot Search FoamTree (2021) to display countries nested within zoogeographic regions (Objective I).

To quantify taxonomic biases (Objective II), we calculated the number and percentage of publications (n, %) reporting each taxonomic Class (Amphibia, Reptilia) and Order (e.g., Anura, Caudata, Squamata, Testudines, Rhynchocephalia).

Results

Geographical biases overview: zoogeographic regions, biomes, countries, and elevational ranges

In the final database of 100 studies, research was recorded across 25 countries, with the highest output concentrated in five nations: the United States ($n=32$; 32%), Brazil ($n=14$), Australia ($n=11$), Colombia ($n=8$), and Ecuador ($n=7$) (Supplementary Material Figures S2 and S3). The Nearctic was the most represented zoogeographic region (33% of publications; $n=33$), followed by the Neotropical ($n=32$), Australian ($n=13$), and Panamanian ($n=10$) regions (Supplementary Material Figures S2 and S3). In contrast, the Palearctic ($n=5$), Sino-Japanese ($n=1$), Oriental ($n=3$) and Madagascan ($n=3$) regions were poorly represented (Fig. 1A; Supplementary Material Table S1). Across the eight biomes, tropical and subtropical moist broadleaf forests were the most represented (47 studies; 47%), followed by temperate broadleaf and mixed forests ($n=35$) (Supplementary Material Table S1). Studies in tropical and subtropical moist broadleaf forests spanned all three elevational bands, whereas temperate broadleaf and mixed forests were only evaluated up to 1,500 m a.s.l. In both biomes, sampling was concentrated in lowlands (<250 m a.s.l.) (Fig. 1A; Supplementary Material Table S2). Notably, only four studies were conducted in high-elevation Andean sites within tropical and subtropical moist broadleaf forests (two in Colombia at 2,100–2,200 m a.s.l. and two in Ecuador at 2,300–3,000 m a.s.l.), underscoring a strong elevational research gap. Overall, most studies were conducted in lowlands (74% conducted below 500 m a.s.l.), predominantly in the Neotropical and Nearctic regions (19 and 17 studies, respectively) (Fig. 1A).

Overview of taxonomic biases at class and order levels

Regarding taxonomic representation, most studies focused on amphibians (60 studies; 60%), with the Anura order being the most frequently analysed ($n=47$), followed by Caudata ($n=25$). No studies were reported on Gymnophiona. For reptiles, 51 studies were identified, addressing the order Squamata ($n=48$), Testudines ($n=3$) and Rhynchocephalia ($n=1$). No studies focused on Crocodylia.

Knowledge shortfalls in ecological response variables used to evaluate edge effects

Overall, 93 studies (93%) reported at least one Prestonian proxy (i.e., occupancy, abundance, population structure, or individual survival), with abundance being the most common (85 studies). Among these population-level metrics, studies most frequently assessed dispersion ($n=13$), occupancy ($n=12$), and population structure ($n=11$), whereas survival was rarely evaluated ($n=5$) (Fig. 2; Supplementary Material Table S3). Despite this focus, explicit demographic analyses—such as temporal population fluctuations, recruitment, and

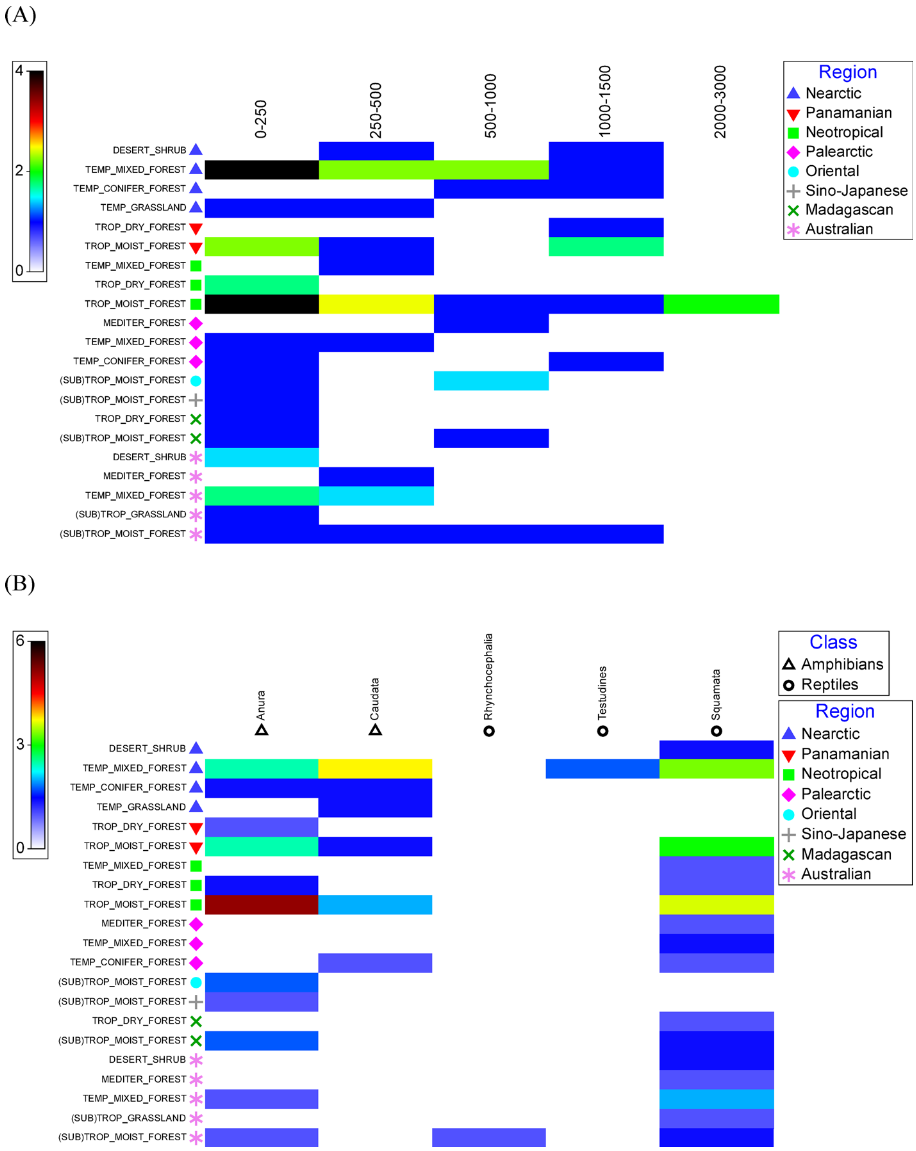

Fig. 1 Biomes and study characteristics of herpetofaunal edge-effect research across zoogeographic regions. Left column shows the eight biome types grouped by eight zoogeographic regions (coloured geometric icons). The three heat maps summarize how frequently each biome was associated with: (**A**) Elevation grouped into five intervalsfrom 0–3000 m a.s.l. to standardize visualization; no studies occurred between 1500–2000 m a.s.l. (**B**) Taxa, studies were classified by Order: Caudata, Anura, and Squamata. Outline symbols indicate Class (triangle = Amphibia, circle = Reptilia); no studies were found for Gymnophiona or Crocodylia. (**C**) Ecological response variables, in which outline symbols indicate which knowledge shortfall each variable can inform (triangle = Prestonian, inverse triangle = Eltonian, square = Hutchinsonian, diamond = Raunkiæran, circle = Darwinian); variables without a shortfall assignment are shown without these symbols. In each heatmap cell colour represents the Whittaker association index between each biome and the corresponding category of analysis (**A**–**C**), calculated from publication frequencies. The colour gradient increases from white (no studies) to blue (low association) to dark tones (high association, interpreted as the highest number of publications). The underlying publication counts ranged from 1–16 in (**A**) elevation, 1–26 in (**B**) Taxa, and 1–24 in (**C**) ecological response variables

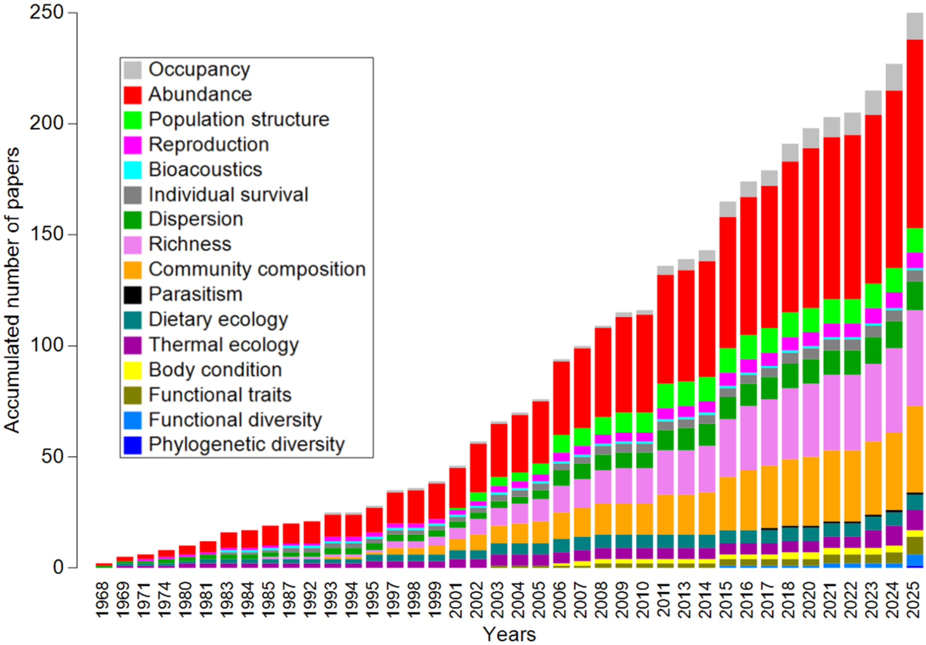

Fig. 2 Cumulative number of publications per year showing ecological response variables used to evaluate edge effects in herpetofauna. Variables that contribute to shortfall assessment are indicated for the following dimensions: Prestonian (occupancy, abundance, population structure, individual survival), Hutchinsonian (thermal ecology), Raunkiæran (body condition, functional traits, diversity), Eltonian (parasitism, dietary ecology), and Darwinian (phylogenetic diversity); remaining variables are not assigned to a shortfall category

long-term demographic trends—were not reported, indicating a remaining gap within the Prestonian shortfall.

In contrast, several frequently reported variables do not map onto the knowledge shortfall framework (Hortal et al. 2015): species richness ($n=43$) and community composition ($n=39$) were common, while reproduction ($n=7$) and bioacoustics ($n=1$) were infrequently assessed (Fig. 2; Supplementary Material Table S3).

Ecological interactions (Eltonian shortfall) were particularly underrepresented: only two studies assessed parasitism and seven examined dietary ecology, even though dietary studies have been published since 1969 (Fig. 2). Regarding ecological niches (Hutchinsonian shortfall), thermal ecology was evaluated in nine studies, also beginning in 1969. Functional approaches (Raunkiæran shortfall) remain limited: functional traits were reported in eight studies (since 2003), body condition in three (since 2006), and functional diversity in five, emerging more recently (since 2015) (Fig. 2). Finally, evidence relevant to the Darwinian shortfall is minimal, with only one recent (2025) study incorporating phylogenetic diversity (Fig. 2; Supplementary Material Table S3).

Geographic Patterns and Taxonomic Coverage as a Proxy for the Wallacean Shortfall

As a proxy for the Wallacean shortfall, we integrated geographic and taxonomic data, revealing marked taxon–biome clustering and a strong geographic research gap. Anurans were studied in seven of eight zoogeographic regions—primarily in the Neotropical ($n=25$), Nearctic ($n=8$), and Panamanian ($n=6$)—but were absent from the Palearctic (Fig. 1B). Caudates were assessed in four regions, overwhelmingly in the Nearctic ($n=18$). Testudines were recorded only in the Nearctic, and Rhynchocephalia (which is restricted to New Zealand) in the Australian region. Squamates were evaluated in six of eight regions, mainly in the Nearctic ($n=13$), Neotropical ($n=12$), and Australian ($n=10$), but were not represented in the Oriental or Sino-Japanese regions (Fig. 1B).

Across biomes, studies were likewise concentrated within the Nearctic, Neotropical, and Australian regions (Fig. 1B). Temperate broadleaf and mixed forests were the only biome represented across all four major groups (Anura, Caudata, Squamata, Testudines), with Testudines occurring exclusively in this biome in our dataset. Squamates were studied in seven of eight biomes—most frequently in tropical and subtropical moist broadleaf forests ($n=20$) and temperate broadleaf and mixed forests ($n=18$)—and were absent only from temperate grasslands, savannas, and shrublands. In contrast, Anura and Caudata were each assessed in four biomes, with the highest concentration of anuran studies in tropical and subtropical moist broadleaf forests ($n=35$) and of caudate studies in temperate broadleaf and mixed forests ($n=14$) (Fig. 1B).

Taxonomic biases in ecological response variables across knowledge shortfalls

Across shortfall dimensions, taxonomic coverage was highly uneven. For the Prestonian shortfall, anurans and squamates were evaluated using all four population-level response variables, dominated by abundance (41 and 38 studies, respectively). Caudates were assessed using three metrics—abundance (24 studies), occupancy (5), and population structure (3)—whereas testudines were represented by only two metrics (abundance, 2 studies; survival, 1 study). The single study on Rhynchocephalia evaluated only abundance (Fig. 3).

Evidence for the Eltonian shortfall was restricted to squamates, with studies addressing species interactions limited to dietary ecology (7 studies) and parasitism (2 studies); no other interaction types (e.g., predation, pollination, seed dispersal) were evaluated. For the Hutchinsonian shortfall, thermal ecology was examined primarily in squamates (7 studies), with limited coverage in anurans (2) and Rhynchocephalia (1). For the Raunkiæran shortfall, functional approaches were scarce and concentrated in anurans (functional traits, 6 studies; functional diversity, 4; body condition, 2), with minimal representation in caudates (1 study each for functional traits, functional diversity, and body condition) and squamates (functional traits, 3; functional diversity, 2). Finally, the Darwinian shortfall was virtually absent, with a single study quantifying phylogenetic diversity in squamates (Fig. 3).

Geographical biases and knowledge shortfalls in edge-effect studies

The association between zoogeographic regions, biomes, and ecological response variables revealed pronounced geographic clustering in the evidence base and persistent knowledge shortfalls in herpetofaunal edge-effect research (Fig. 1C). Within the Prestonian shortfall,

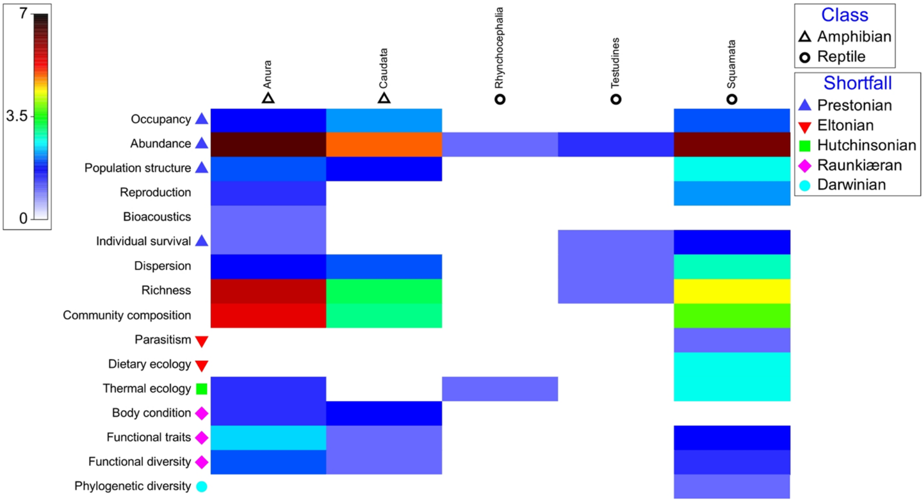

Fig. 3 Ecological response variables used to assess edge effects across herpetofaunal orders Caudata (salamanders), Anura (toads and frogs), Squamata (snakes and lizards), Testudines (turtles and tortoises), and Rhynchocephalia (tuataras). Outline symbols indicate taxonomic Class (empty triangle = Amphibia, empty circle = Reptilia). In the heat map showing the frequency of 16 ecological response variables (rows), the coloured geometric symbols indicate which knowledge shortfall each variable can inform (blue triangle = Prestonian, inverse red triangle = Eltonian, green square = Hutchinsonian, purple diamond = Raunkiæran, light blue circle = Darwinian); variables without a shortfall assignment are shown without these symbols. Cell shading represents the association between each ecological response variable and taxonomic order, calculated using the Whittaker index from publication frequencies; the colour gradient increases from lighter to darker tones, with darker tones indicating a higher number of publications (n = 38–41 studies)

abundance was the only metric evaluated across all regions and biomes, but it was strongly concentrated in Nearctic temperate broadleaf and mixed forests (n = 24) and Neotropical tropical and subtropical moist broadleaf forests (n = 21). Other population-level metrics were far less widespread: occupancy and population structure were reported across only five to six biomes, again with the highest frequency in Nearctic temperate broadleaf and mixed forests (n = 6 and n = 4, respectively), whereas reproduction and survival were each assessed in only three biomes.

Variables informing the Eltonian shortfall were nearly absent and geographically idiosyncratic: parasitism was evaluated only twice, in Australian tropical and subtropical grasslands, savannas, and shrublands and in Panamanian tropical and subtropical moist broadleaf forest. For the Hutchinsonian shortfall, thermal ecology was reported in a limited set of biome–region combinations, primarily in tropical and subtropical moist broadleaf forests across three regions (Australian, n = 1; Neotropical, n = 4; Panamanian, n = 2), and sparsely in the Nearctic (temperate broadleaf and mixed forests, n = 1; temperate conifer forests, n = 1). Evidence for the Raunkiæran shortfall was similarly restricted: body condition was assessed only once per biome in Nearctic temperate broadleaf and mixed forests, Nearctic temperate conifer forests, and Neotropical tropical and subtropical moist broadleaf forests; functional traits were measured only in the Neotropics (tropical and subtropical moist broadleaf forests, n = 6; tropical and subtropical dry broadleaf forests, n = 2); and functional diversity was reported in Neotropical moist (n = 3) and dry broadleaf forests (n = 1), plus one

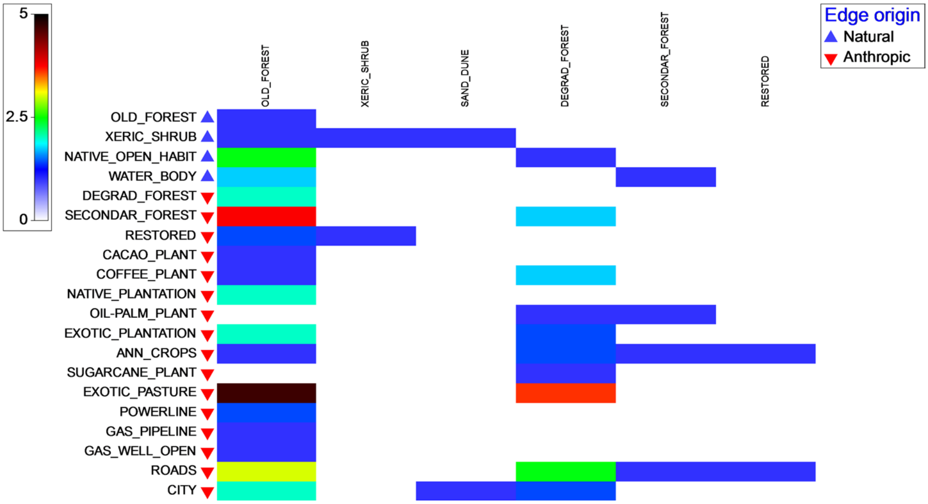

Fig. 4 Matrix–native vegetation pairings in herpetofaunal edge-effect studies. Heat map showing the frequency of studies conducted at the interface between 20 natural and anthropogenic matrix types (rows) and six native vegetation cover types used as the reference (or control habitat in the study design) (columns). Cell shading represents Whittaker's association index calculated from publication frequencies derived for each matrix–vegetation pairing; the colour gradient (shown in the legend) increases from lighter to darker tones, with darker tones indicating higher frequencies (equivalent to 22 publications). The analysis highlights a strong concentration of studies in a limited set of pairings (e.g., exotic pastures or secondary forest as matrices contrasted with old-growth forest interiors), while other matrices (e.g., gas/powerline/road infrastructure, cities, crops/plantations) and reference or control vegetation types (e.g., xeric shrublands, restored areas, secondary forest, sand dunes) remain comparatively underrepresented

study in Panamanian moist broadleaf forests. Finally, evidence relevant to the Darwinian shortfall was minimal, with a single study quantifying phylogenetic diversity in Neotropical tropical and subtropical moist broadleaf forests (Fig. 1C).

Edge contexts: matrix types and reference habitats across studies

The association between adjacent matrix types and native vegetation reference habitats revealed consistent patterns in how herpetofaunal edge effects have been evaluated (Fig. 4). Among the 14 anthropogenic land-cover types reported, the most frequently studied matrices were exotic pastures (35 studies), followed by secondary forest and roads (17 studies each). These matrices were most often contrasted against forest interiors classified as old-growth, degraded, or secondary forest, which together comprised the dominant set of reference/control habitats (Fig. 4). By comparison, natural matrices were seldom considered and were represented by only six categories: native open habitats ($n=7$), degraded forest ($n=4$), native forestry plantations ($n=4$), water bodies ($n=4$), old-growth forest ($n=1$), and xeric shrublands ($n=1$). From the reference-habitat perspective, studies used six native vegetation types, with old-growth forest serving as the interior control in 81% of studies and degraded forest in 34% (Fig. 4).

Discussion

In this review, we synthesize global evidence on edge effects in amphibians and reptiles, utilizing the biodiversity "knowledge shortfalls" framework to identify critical biases (Hortal et al. 2015). Although habitat transformation continues to reshape ecological communities worldwide (Palmeirim et al. 2017; Tan et al. 2023), the ecological consequences of edges remain difficult to generalize. Responses are strongly context-dependent and mediated by factors such as matrix permeability, microclimate, and edge contrast (Ries et al. 2004). Our results reveal consistent geographic, taxonomic, and thematic gaps that constrain inference across regions and biomes, mirroring variability reported in broader global syntheses (Schneider-Maunoury et al. 2016; Pfeifer et al. 2017; Willmer et al. 2022). Below, we discuss how the current evidence contributes to reducing specific shortfalls, where blind spots persist, and how targeted research can strengthen conservation guidance in fragmented landscapes.

Geographic biases and the influence of edge context

Our synthesis highlights a marked geographic bias in herpetofaunal edge-effect research, driven by uneven coverage across zoogeographic regions, biomes, and elevational ranges. This unevenness matters because the ecological consequences of landscape transformation are not globally uniform, and fragmentation impacts may be stronger in some contexts than others (Betts et al. 2019; Franklin et al. 2021). While tropical studies constitute a substantial portion of the literature reviewed, highly cited contributions remain disproportionately associated with temperate realms (Supplementary Material Table S4 and Figure S4A), suggesting that widely used generalizations about edge sensitivity may be shaped by a subset of temperate case studies. This could limit transferability to tropical regions, where biodiversity losses under land-use change can be particularly severe (Betts et al. 2019; Pöpperl and Seidl 2021). Although citation counts are an imperfect proxy of scientific attention, as they may be influenced by publication age and broader field dynamics, they still reveal a consistent asymmetry in visibility across geographic domains (Supplementary Material Table S4). Citation patterns are also uneven across elevation bands and within tropical regions: in high-elevation systems, a small number of studies, particularly Gibbs (1998), account for much of the visibility in the literature (Supplementary Material Figure S4B), whereas Panamanian studies receive substantially more citations than those from the broader Neotropical region despite similar publication numbers (Supplementary Material Figure S4C). Together, these citation patterns suggest that global syntheses and conservation guidance may be disproportionately influenced by a few highly visible studies, potentially overshadowing broader ecological patterns in edge effects on amphibians and reptiles.

Geographic bias in both publications and citations is compounded by a lack of data on how edge effects vary along elevational gradients. Current evidence suggests that amphibian responses can be highly variable, with lowland and highland systems often differing in the strength and mechanisms of edge effects (Gascon et al. 1999; Toral et al. 2002). In tropical montane cloud forests, persistent mist and high humidity may buffer edge-related microclimatic fluctuations, resulting in minimal differences in species composition between the edge and forest interior (Cortés et al. 2008; Isaacs-Cubides and Urbina-Cardona 2011). However, the surrounding matrix—particularly open pastures—can generate extreme abiotic conditions that strongly limit the movement of high-mountain herpetofauna beyond native forest remnants (Marsh and Pearman 1997; Galindo-Uribe et al. 2022). Conversely, in Neotropical rainforest lowland ecosystems, year-round humidity and rainfall may mitigate edge effects at the forest–matrix interface, facilitating the movement and reproduction of generalist species (Pearman 1997; Gascon et al. 1999). Notably, our database shows a conspicuous absence of studies in the 1,500–2,000 m elevational band, suggesting that research effort has been concentrated in lowlands or in a limited number of high-elevation sites. This gap deserves attention because edge-effect direction and magnitude are shaped by interacting global and local drivers, including matrix contrast and the distance between edge and 'interior' sampling locations (Willmer et al. 2022).

Importantly, the physical structure of the matrix mediates herpetofaunal responses to the cascade of edge-driven changes in vegetation structure and microhabitat conditions—such as canopy cover, leaf-litter cover, understorey density, and temperature—that shape microclimatic quality along forest–matrix ecotones (Urbina-Cardona et al. 2006). "Soft edges" created by matrices structurally like the native ecosystem (e.g., certain forestry plantations) can mitigate negative impacts, allowing species to inhabit edges even if they cannot disperse into the matrix (Santos-Barrera and Urbina-Cardona 2011; López-Bedoya et al. 2022). Despite the importance of matrix type, only a small fraction of studies explicitly compared different anthropogenic matrices (e.g., de Maynadier and Hunter 1998; Ferreira et al. 2016). Future research should prioritize meta-analytic and other quantitative synthesis approaches (and, where possible, standardized comparative study designs) that explicitly test how elevation and ecosystem type (e.g., moist vs. dry forests) modulate edge effects while accounting for land-use contrast.

Taxonomic gaps and mechanistic trait-based responses

The geographic and contextual gaps described above are reinforced by a clear taxonomic bias in edge-effect studies: taxa are unevenly represented, with a strong skew toward Anura and Squamata, while groups such as Gymnophiona and Crocodylia remain virtually absent. This taxonomic gap limits generalization because edge sensitivity is mediated by lineage-specific ecophysiology and life-history strategies (Ries et al. 2004; Schneider-Maunoury et al. 2016). For instance, amphibians often exhibit narrow thermal safety margins and a strong dependence on environmental humidity, increasing vulnerability to microclimatic shifts near edges (Posse-Sarmiento and Banks-Leite 2024). In contrast, many reptiles possess adaptations (e.g., keratinized skin) that can confer greater tolerance to drier, warmer conditions typical of some anthropogenic matrices (Nowakowski et al. 2018).

Understanding these responses requires addressing the Raunkiæran (functional traits) and Hutchinsonian (thermal tolerance) shortfalls. Traits related to dispersal ability, thermal regulation, and reproductive strategies can act as filters across forest–matrix gradients. For example, anuran reproductive modes can influence persistence: species with aquatic larvae may utilize artificial water bodies in modified lowlands, whereas direct-developing species may be restricted to core forest areas (Pineda et al. 2005). Current research on functional diversity, although still limited, suggests that anthropogenic edges can act as ecological filters (Carvajal-Cogollo and Urbina-Cardona 2015; Granda-Rodriguez et al. 2025), disproportionately affecting functionally rare species associated with the core areas of mature forests (Palomino-Cuéllar and Urbina-Cardona 2025). Because these rare species often harbor extreme functional trait values, their loss from assemblages can disproportionately erode the functional diversity of the ecological community (Zabala-Forero et al. 2025). In modified landscapes, environmental filtering may favour stress-tolerant species in the matrix (e.g., pastures), whereas in forest interiors, strong positive relationships between species richness and functional diversity suggest niche differentiation, with newly added species contributing distinct trait combinations rather than redundant ones, a pattern consistent with limiting similarity mechanisms (Palomino-Cuéllar and Urbina-Cardona 2025). Expanding functional-trait research to underrepresented groups is essential to move beyond simple species lists toward a mechanistic understanding of vulnerability.

The prestonian shortfall: from abundance to demographic persistence

Edge-effect research on herpetofauna exhibits a persistent Prestonian shortfall, characterized by heavy reliance on community-level descriptors such as species richness and abundance (Magurran and McGill 2010). While these metrics provide rapid snapshots of biodiversity, they offer limited insight into long-term persistence, reproductive success, or recruitment—processes that ultimately govern population viability in fragmented landscapes (Díaz et al. 2013). Our results indicate that demographic parameters (e.g., survival rates and population structure) remain comparatively understudied, likely reflecting the logistical and financial constraints of long-term monitoring and mark–recapture approaches (Bragg et al. 2005).

This gap is important because edge-related increases in species abundance and richness may be driven by spillovers by generalist and invasive species favored by edge-induced microclimatic change, making local counts a poor proxy for habitat quality for resident forest populations (Ries et al. 2004; Granda-Rodriguez et al. 2025). Moreover, few studies link abundance patterns to health-related indicators such as body condition, which can provide a robust proxy for physiological stress and fitness (Blouin-Demers et al. 2007). Meta-analytic evidence indicates that body condition consistently declines under disturbance (Macdonald et al. 2023), providing an early-warning indicator of edge-related stress before population-level changes are detectable. Integrating body condition and other health metrics into edge-effect studies could improve early detection of sublethal impacts that may precede demographic decline. Bridging the Prestonian shortfall will require greater emphasis on study designs that combine population monitoring with health and performance metrics to better predict trajectories under continued fragmentation.

Neglected dimensions: species interactions and evolutionary history

The largest knowledge gaps identified in our review correspond to the Eltonian (interactions) and Darwinian (evolution) shortfalls. Biotic interactions—such as parasitism, predation, and competition—are fundamental to ecosystem function yet remain largely unexplored in edge contexts, especially in high biodiversity regions (Schlaepfer and Gavin 2001; Gonçalves-Souza et al. 2023; López-Bedoya et al. 2024). The local extinction of amphibians, for example, can trigger trophic cascades that alter nutrient cycling and reduce prey availability for higher-order predators such as snakes (Whiles et al. 2013; Zipkin et al. 2020). Without data on how edges alter these networks, the functional consequences of habitat fragmentation and extinction debts may be underestimated.

Similarly, the Darwinian shortfall limits understanding of how evolutionary history shapes responses to ecological change (Diniz-Filho et al. 2013). The marked absence of phylogenetic diversity studies in edge contexts ($n=1$) likely reflects the specialized analytical skills, computational resources, and lack of molecular data often required for phylogenetic assessments (Soares et al. 2023); expertise not yet widely integrated into edge-effect studies on herpetofauna. Although detecting microevolutionary shifts at the temporal scales of most edge studies is challenging, edges can generate novel selective pressures that may contribute to rapid change in traits linked to tolerance (e.g., desiccation resistance) (Skelton et al. 2024). In addition, incorporating phylogenetic diversity metrics can reveal whether edge-driven turnover involves non-random loss of evolutionary heritage (de la Sancha et al. 2023). Addressing these dimensions does not necessarily require long-term evolutionary experiments; rather, it can be advanced by integrating phylogenetic frameworks and interaction-network approaches into standard ecological assessments.

Conclusions

Our global synthesis reveals persistent geographic, taxonomic, and ecological gaps in edge-effect research on amphibians and reptiles, confirming multidimensional knowledge shortfalls that constrain understanding of species responses to landscape transformation and habitat fragmentation. The evidence base is heavily skewed toward community-level metrics (e.g., richness, abundance) for anurans and squamates, particularly in Nearctic and Neotropical lowlands, leaving several biomes—especially high-elevation systems and some open or arid habitats—and multiple lineages underrepresented, including the absence of caecilians and crocodylians and the very limited representation of Testudines and Rhynchocephalia. Consequently, the generalization of edge impacts remains constrained by limited evidence on demographic, physiological, and interaction-based mechanisms that ultimately determine extinction risk.

To advance the field, research should shift from predominantly descriptive assessments toward process-based approaches that address specific knowledge gaps. Bridging the Prestonian, Hutchinsonian, Raunkiæran, and Eltonian shortfalls will require integrating demographic inference, physiological thresholds, functional traits (including body condition), and biotic interactions into study designs. Furthermore, despite constraints of spatial and temporal scale, incorporating phylogenetic frameworks may help reduce the Darwinian shortfall by clarifying how evolutionary history shapes resilience to environmental change. From a conservation perspective, our synthesis indicates that current evidence is not yet balanced enough across regions, taxa, and response dimensions to support strong generalizations—or to rank management actions—regarding edge mitigation for herpetofauna. This underscores the need for targeted, long-term monitoring and hypothesis-driven studies in underrepresented contexts (e.g., high-elevation systems, open/arid biomes, and poorly studied lineages) that jointly quantify demographic, physiological, and interaction-based mechanisms. Strengthening this evidence base will enable more robust, context-specific guidance for land-use planning and adaptive management in anthropogenically transformed landscapes.

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Author contributions Conception and design of the study by LMHR, NUC and PALB; Data collection and analysis were performed by NUC, LMH and PALB. NUC prepared Figs. 1, 2, 3 and 4 and S2 and S4, LMH prepared figures S1 and S3. The first draft of the manuscript was written by LMHR and NUC, and all authors commented on previous versions of the manuscript. All authors read and approved the final version of the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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